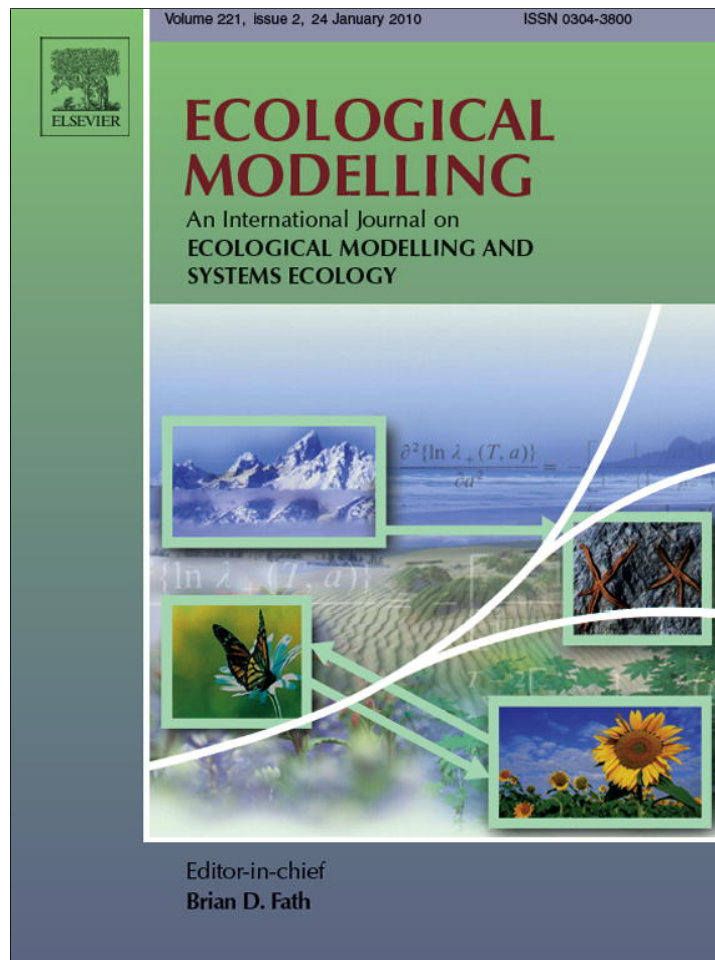


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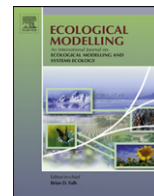
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Measuring and modeling the seasonal changes of an urban Green Treefrog (*Hyla cinerea*) population

Azmy S. Ackleh^{a,*}, Jacoby Carter^b, Lauren Cole^c, Tom Nguyen^a, Jay Monte^a, Claire Pettit^a

^a Department of Mathematics, University of Louisiana at Lafayette, Lafayette, LA 70504, USA

^b U.S. Geological Survey National Wetlands Research Center, Lafayette, LA 70506, USA

^c Department of Biology, University of Louisiana at Lafayette, Lafayette, LA 70504, USA

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ABSTRACT

Green Treefrogs (*Hyla cinerea*) were captured, marked, measured and released at an urban study site in Lafayette, LA, during the 2004 and 2005 breeding seasons. A statistical method based on a generalization of the hypergeometric distribution was used to derive weekly time-series estimates of the population sizes. To describe the population dynamics, a stage structured mathematical model was developed and compared to time-series obtained from the weekly population estimates study using a least-squares approach. Two fitting experiments were done: (1) Using uniform distribution for the birth rate during the breeding season; (2) Using a birth rate distributed according to weekly data on frog calling intensity. Although both model-to-data fits look very promising during the years 2004 and 2005 and result in similar inherent survivorship rates for the tadpoles, juvenile and adult frogs, the fit that uses the calling data predicts a lower number of tadpoles and frogs in the long term than the one that uses uniform birth distribution. The parameter estimates resulting from these fitting experiments are used in the context of stochastic simulations to derive extinction and persistence probabilities for this population. Due to the oscillatory dynamics (with high amplitude) evidenced by the capture–recapture data and corroborated by the model, it is suggested that anuran monitoring efforts should take into account the natural intra-annual variation in population size.

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1. Introduction

An apparent global decline of amphibians has created concern, which has led to numerous research efforts (Bridges and Dorcas, 2000; de Solla et al., 2006; Bailey et al., 2004; Lips et al., 2003; Pellet et al., 2006). Many of these efforts focus on monitoring amphibian populations to better understand their dynamics (Bailey et al., 2004). In order to determine whether there is a decline, it is essential to accurately and efficiently determine their population size (Driscoll, 1998). However, because of their natural history, local populations of amphibians may fluctuate during the course of the year. First because many amphibian species are explosive breeders, that is they have large number of progeny in short periods of time (e.g., Dundee and Rossman, 1989). Second, many amphibian species life history are characterized by adults migrating to breeding sites and juveniles migrating out of those sites to habitat occupied by adults (McDiarmid, 1994). Tracking these fluctuations will be important if we are to interpret year-to-year changes in population size.

Our research efforts focus on the Green Treefrog (*Hyla cinerea* Schneider, 1799) which is found throughout the southeastern region of the United States (Dickerson, 1969). In Louisiana, these frogs are found in freshwater ponds used as breeding sites throughout the state (Dundee and Rossman, 1989). At the study site (see description below), adult *H. cinerea* can be found on emergent vegetation such as Cattail (*Typha* spp. L.) and Bull-tongue (*Sagittaria lancifolia* L.) as well as on nearby trees and on windows and the sides of buildings. Adult *H. cinerea* range in length from 37 to 63 mm (Wright and Wright, 1949). At the study site, *H. cinerea* have been noted to call from April through September.

We had two questions we wanted to explore with this study. First, how did the population of *H. cinerea* change throughout the year? While this question was partially answered in Pham et al. (2007), we wanted to see if the same intra-annual patterns observed in 2004 would be repeated in 2005. Second, we wanted to use the estimations made of the life history parameters to determine if the population under study will remain persistent over a long period of time. A model is necessary to answer the second question since the population fluctuates throughout the year and therefore point estimations are not predictive without an understanding of the intrinsic dynamics.

* Corresponding author. Tel.: +1 337 482 6709; fax: +1 337 482 5346.
E-mail address: ackleh@louisiana.edu (A.S. Ackleh).



Fig. 1. Aerial view of the federal office complex in Lafayette, LA, USA with ponds used in the study highlighted. The coordinates of pond D are 30.2246° N, 92.045° W.

We used two approaches to study the dynamics of this urban population: (1) The use of a mark-capture–recapture procedures and generalized hypergeometric statistical method described in Pham et al. (2007) and Yang and Pal (2009) for data collected during the 2004 and 2005 breeding season supplemented with frog call monitoring for the 2005 sampling season; (2) The development of a three stage discrete-time mathematical model to understand the long-time behavior of this population. To derive estimates for the life-history parameters, the model was fitted to the population estimates obtained from the capture–recapture data through a non-linear least-squares approach. These estimates were then used to study the long-time behavior.

2. Study area

Our study site is in the city of Lafayette, LA, USA, and is a collection of artificial ponds and reflecting pools at the USGS National Wetlands Research Center (NWRC) and the National Marine Fisheries Service' Estuarine Habitats and Coastal Fisheries Center (EHCFC), henceforth the 'Federal Complex' (see Fig. 1). In 1992, the NWRC was built, and the ponds in front of the complex were created. In 1999, when the EHCFC was built next door, the ponds around the perimeter of the complex were created. The landscape surrounding these ponds is representative of various fresh water wetland vegetation types with elements that include Willow (*Salix* spp. L.), Cattail (*Typha* spp.), Bald Cypress (*Taxodium distichum* L. Rich.), and Bulltongue (*Sagittaria* spp.). There are seasonal wetlands located in the fields neighboring the complex, but the nearest is 60 m away and access to it is limited by the buildings. The eastern border of the ponds is comprised of sidewalks, four-lane roads, and is located across the street from a medium density housing complex. Thus, while this population is in an urban area, the degree to which it represents a typical urban population is unclear. However, because it is functionally isolated it is a good population to study the dynamics for without concern of significant immigration due to the absence of nearby breeding sites.

3. Methods

3.1. Capture–recapture study and hypergeometric statistical method

The 2004 capture–recapture study used Visible Implant Elastomer (VIE) tags to mark frogs in weekly cohorts (Pham et al., 2007). In 2005, mark-recapture was conducted once a week for 19 weeks, from April through September at the Federal Complex and used VI-alpha tags (Northwest Marine Technology Inc., 2002) in place of VIE. The change was made in order to follow individual capture histories, which the VIE tags do not allow. At least 30 min after sunset and before attempting to hand capture frogs, we recorded current

weather conditions and the intensity of frog calls using North American Amphibian Monitoring Program protocols (NAAMP, 2008). The frog calling intensity scale runs from 0 to 3: 0 – no frogs are calling; 1 – individuals can be counted and there is space between calls; 2 – calls of individuals can be distinguished but there is some overlapping of calls; 3 – full chorus, calls are constant, continuous and overlapping. After monitoring frog calls, we conducted time constrained searches in and around each of the four ponds in the complex for *H. cinerea*. Frogs were caught by hand during a search of the vegetation and adjacent vertical surfaces such as walls and windows. Frogs caught during the search were held in individual clear plastic bags with zipper seals until they could be measured for length and checked for tags. Body length was used to determine the life history stage of the frog, smaller frogs and frogs with tail remnants considered juvenile (Pham et al., 2007). Unmarked frogs were marked and all frogs were released in the general area where they were caught. Because we wanted to compare population estimates for 2004 and 2005 it was necessary to use the generalized hypergeometric maximum likelihood estimation method described in Pham et al. (2007) and Yang and Pal (2009) to derive weekly population estimates.

3.2. Discrete-time population model

To develop a discrete-time model which describes the dynamics of the urban *H. cinerea* population, we divided the population into three different stages: tadpoles, non-breeders, and breeders. Let the number of tadpoles at time t be denoted by T_t , the number of non-breeders be denoted by N_t , and the number of breeders be denoted by B_t . The breeding season for *H. cinerea* lasts approximately 6 months in Louisiana. The tadpole stage starts at the time eggs are laid and fertilized and ends when the tadpole metamorphoses to a froglet. A frog is classified as a non-breeder from the froglet stage through to the next breeding season. In our model a frog is a tadpole for 5 weeks (Garton and Brandon, 1975; Blouin, 1992; Gunzburger, 2006; Smith, 2005; Leips and Travis, 1994; Duellman and Trueb, 1986) and after 1 year (52 weeks), a non-breeder becomes a breeder (Garton and Brandon, 1975). Furthermore, for anuran populations, tadpoles only compete with tadpoles for resources, and non-breeders and breeders compete amongst each other for resources. Thus, survivorship of tadpoles depends on the tadpole density while survivorship of non-breeders and breeders depends on the total density of non-breeders and breeders. Because our field data were collected once a week we set the time unit in our model to 1 week. We further structure the tadpoles and non-breeding stages by age. Because tadpoles take 5 weeks to metamorphose into a frog, so we use five age classes of tadpoles, each of which is 1 week long and denoted by T_t^a , $a = 1, \dots, 5$. Also, it takes 52 weeks for a juvenile frog to sexually mature, so we assume 52 age classes for non-breeders each of which is 1 week

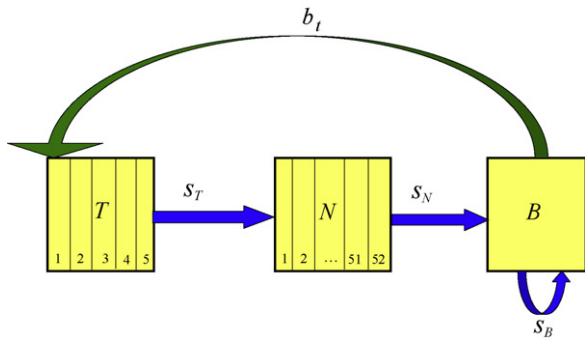


Fig. 2. Conceptual diagram of the model (1).

long and denoted by N_t^a , $a = 1, \dots, 52$. Thus, the total tadpoles and non-breeders at time t are given by $T_t = \sum_{a=1}^5 T_t^a$ and $N_t = \sum_{a=1}^{52} N_t^a$, respectively. See Fig. 2 for a conceptual diagram of this model.

The model for the dynamics of this population is described by the difference equations

$$\begin{aligned} T_{t+1}^1 &= b_t B_t \\ T_{t+1}^{a+1} &= S_T(T_t) T_t^a & a = 1, \dots, 4 \\ N_{t+1}^1 &= S_T(T_t) T_t^5 \\ N_{t+1}^{a+1} &= S_N(F_t) N_t^a & a = 1, \dots, 51 \\ B_{t+1} &= S_N(F_t) N_t^{52} + S_B(F_t) B_t \end{aligned} \quad (1)$$

Here, $F_t = N_t + B_t$ is the total number of frogs at time t . The function b_t is the time-dependent birth rate which is equal to the number of tadpoles produced by one breeding frog per unit-time (taken to be 1 week in our model to match the capture–recapture data) during the breeding season (and zero otherwise). Thus, due to seasonality in birth our model is non-autonomous. The functions, S_T , S_N and S_B , are the (density-dependent) fractions of surviving juveniles, non-breeding adults and breeding adults per unit-time (1 week). For this model, we will utilize Beverton–Holt type density-dependent functions given as follows (Caswell, 2001; Allen, 2007):

$$S_T(T) = \frac{a_1}{1 + k_1 T}, \quad S_N(F) = \frac{a_2}{1 + k_2 F}, \quad S_B(F) = \frac{a_3}{1 + k_3 F} \quad (2)$$

Note that the constants, a_1 , a_2 and a_3 , represent the inherent survivorship of tadpoles, non-breeders and breeders, respectively. The above model can be written in a nonlinear time-dependent matrix form (Cushing, 1998; Caswell, 2001) as follows:

$$x_{t+1} = A(t, x_t) x_t \quad (3)$$

where the coefficient matrix A is a 58×58 matrix whose nonzero elements are given by:

$$\begin{aligned} A_{1,58} &= b_t \\ A_{i,i-1} &= S_T(T_t), \quad i = 2, \dots, 6 \\ A_{i,i-1} &= S_N(F_t), \quad i = 7, \dots, 58 \\ A_{58,58} &= S_B(F_t) \end{aligned}$$

and $x_t = [T_t^1, \dots, T_t^5, N_t^1, \dots, N_t^{52}, B_t]^{\text{transpose}}$ is a 58×1 vector.

3.3. Parameter estimation method

Information about the birth rate was obtained from the literature. In one breeding season, *H. cinerea* can produce a wide range of clutch sizes with an average of about 800 eggs (Gunzburger, 2006; Dundee and Rossman, 1989; Garton and Brandon, 1975; Perrill and Daniel, 1983). *H. cinerea* females may produce 1–2 clutches per breeding season (Perrill and Daniel, 1983; Morrison and Hero, 2003). While the data for clutch size are relatively good,

we could not find studies with estimates of either egg or tadpole survival rates (NEPARC, 2009). Furthermore, experimental studies indicate that tadpole survivorship can be highly variable depending on both the predator community and kinds of refugia available (Gunzenburger and Travis, 2004, 2005). Therefore, for the purpose of our models we arbitrarily assume that 50% of the eggs hatch to become tadpoles, i.e., eggs survivorship which we denote by a_0 is fixed at 0.5. Thus based on the assumption that each female produces on average 1200 eggs (one and a half clutches), we assume in our computations that each breeding adult produces around 300 tadpoles during the breeding season assuming the ratio between females and males to be 1:1. If, for example, we assume a uniform breeding distribution during the 26 week breeding season (number of weeks in the breeding season of 6 months), then we get a mean production per week to be $b_t = 11.538$ during the 26 weeks of the breeding season and zero otherwise.

The rest of the model parameters are not available in the literature, so we combine the knowledge gained in the field with the current modeling efforts to infer some information about these unknown parameters. In particular, we set up the following least-squares problem: Given data(t_i), the frog population estimate from capture–mark–recapture data at week t_i , we want to find the 6×1 parameter vector $q = [a_1, k_1, a_2, k_2, a_3, k_3]^{\text{transpose}}$ that minimizes the following weighted least-squares function L :

$$L(q) = \sum_{i=1}^n [\log(\text{data}(t_i) + 1) - \log(F_t(q) + 1)]^2, \quad (4)$$

where $F_t(q) = N_t(q) + B_t(q)$ is a quantity representing the total number of frogs (breeders and non-breeders) at time t which can be calculated from the solution of the population model (1). This quantity depends on the vector value $q = [a_1, k_1, a_2, k_2, a_3, k_3]^{\text{transpose}} = [q_1, q_2, q_3, q_4, q_5, q_6]^{\text{transpose}}$ and n is the number of data points available. Because of the high amplitude oscillations in the population dynamics evidenced by the population estimates we used a weighted least-squares function. Using the routine “lsqnonlin” in the software MATLAB, we determine the numerical values for these parameters.

Once parameter estimates are obtained we can compute standard errors for q . This can be done using similar ideas from standard regression formulations in statistics (Bates and Watts, 1988; Gallant, 1987; Huet et al., 2003). To obtain this analysis, we need to compute the sensitivity matrix

$$X(q) = \begin{bmatrix} \frac{(\partial/\partial q_1)F_{t_1}}{1 + F_{t_1}} & \frac{(\partial/\partial q_2)F_{t_1}}{1 + F_{t_1}} & \dots & \frac{(\partial/\partial q_6)F_{t_1}}{1 + F_{t_1}} \\ \frac{(\partial/\partial q_1)F_{t_2}}{1 + F_{t_2}} & \frac{(\partial/\partial q_2)F_{t_2}}{1 + F_{t_2}} & \dots & \frac{(\partial/\partial q_6)F_{t_2}}{1 + F_{t_2}} \\ \vdots & \vdots & \ddots & \vdots \\ \frac{(\partial/\partial q_1)F_{t_n}}{1 + F_{t_n}} & \frac{(\partial/\partial q_2)F_{t_n}}{1 + F_{t_n}} & \dots & \frac{(\partial/\partial q_6)F_{t_n}}{1 + F_{t_n}} \end{bmatrix}, \quad (5)$$

Since we cannot compute $(\partial/\partial q_j)F_{t_i}$, $j = 1, 2, \dots, 6$, $i = 1, 2, \dots, n$ directly from our model, we use the following forward difference approximation:

$$D_{ij}^{j+}(F_{t_i}) = \frac{1}{h} (F_{t_i}(q_j + h) - F_{t_i}(q_j)), \quad j = 1, 2, \dots, 6, \quad i = 1, 2, \dots, n \quad (6)$$

where h is taken to a small positive constant. With these difference approximations we are able to compute an approximation to the sensitivity matrix $X(q)$ denoted by $\hat{X}(q)$.

Under the assumptions of classical nonlinear regression theory, we know that if $\hat{\epsilon}_i \sim \mathcal{N}(0, \sigma^2)$, where $\hat{\epsilon}_i$ is the difference between the observation and the model at time t_i , then the least-squares

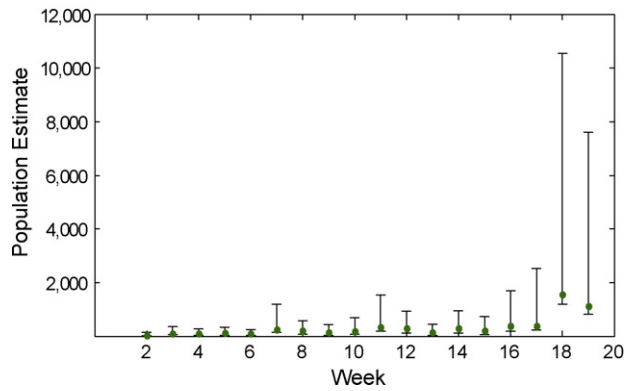


Fig. 3. Time-series plot of the estimated frog population numbers in 2005 with the 95% confidence intervals.

estimate q^* is expected to be asymptotically normally distributed. In particular, for large samples we may assume

$$q^* \sim \mathcal{N}(q_0, \sigma^2 \{X^T(q_0)X(q_0)\}^{-1}), \tag{7}$$

where q_0 is the true minimizer and $\sigma^2 \{X^T(q_0)X(q_0)\}^{-1}$ is the true covariance matrix (Davidian and Giltinan, 1995; Bates and Watts, 1988; Gallant, 1987; Huet et al., 2003). Since we do not have q_0 and σ^2 , we follow a standard statistical practice (Huet et al., 2003; Ackleh et al., 2005; Adams et al., 2005): substitute the computed estimate q^* for q_0 and approximate σ^2 by

$$\hat{\sigma}^2 = \frac{1}{n-6} \sum_{i=1}^n [\log(\text{data}(t_i) + 1) - \log(F_{t_i}(q) + 1)]^2. \tag{8}$$

Then we take $\sqrt{(\hat{\sigma}^2 \{\hat{X}^T(q^*)\hat{X}(q^*)\}^{-1})_{j,j}}$ to be the standard deviation for the parameter $q_j, j = 1, 2, \dots, 6$.

4. Results

4.1. Results from capture–recapture study

In Fig. 3 we present the weekly frog (non-breeders and breeders) population estimates and the 95% confidence intervals resulting from the hypergeometric statistical method (Pham et al., 2007). In week 2 of the 2005 dataset (May 6, 2005) we obtained the smallest frog population estimate, 35, and in week 18 (September 10, 2005) we obtained the largest frog population estimate, 1559. In 2004, the smallest population size was estimated to be 123, in week 10 (June 28, 2004) and the largest population size was estimated to be 1429 in week 11 (August 27, 2004). Since the dynamics of each population change as the dataset encounters the steep increase, we break up the populations into two sets, before and after the increase. In 2005, the average population size before the steep increase, weeks 2–17, is 205 frogs, and the average population size for week 18 and 19 is 1343 frogs. In 2004, the average population size before the steep increase, weeks 2–10, is 173 frogs and the average population size for weeks 11–18, after the steep increase, is around 564 frogs.

In Table 1 the average lengths of the frogs are recorded as well as the smallest and largest frog for each week. In 2005, the smallest frog caught was 20 mm and in contrast with 2004, where the smallest frog caught was 15 mm (Pham et al., 2007). The largest frog caught in 2005 was 60 mm and in 2004, the largest frog caught was 55 mm (Pham et al., 2007). In 2005, before week 18, the average of the mean lengths of the frogs for each week was 44.4 mm. Weeks 18 and 19 produced an average length of 30.2 mm. A similar pattern was observed in the 2004 dataset. Before the steep increase

Table 1

Minimum, maximum, and average lengths of frogs caught during the 2005 sampling season. There were 224 capture events during the 2005 sampling season.

Week #	n	Min (mm)	Max (mm)	Median	Mean	S.D.
1	18	41	58	49	48.7	6.2497
2	6	34	51	36	40.3	9.2916
3	26	22	52	41	39.7	8.0770
4	13	33	57	49	48.0	6.1373
5	17	30	55	45	45.4	6.9107
6	15	36	60	44.5	45.1	6.5850
7	8	35	51	46.5	45.0	5.6821
8	26	33	57	45	45.1	6.7634
9	12	38	57	46	45.3	6.1398
10	6	36	50	45	43.7	6.4704
11	7	36	50	45	45.1	4.9809
12	18	36	56	45	46.3	4.8118
13	5	34	57	48	47.2	8.3487
14	13	40	51	45	44.7	3.4250
15	5	40	52	46	46.2	4.2661
16	6	30	50	42.5	41.7	8.5010
17	3	25	52	36	37.7	13.5769
18	12	23	48	29.5	31.7	8.3811
19	8	20	37	29.5	28.6	6.2092

in week 11, the average length was 34.0 mm and after week 11, the average length was 28.7 mm. This decrease in frog length average, concomitant with the increase in numbers caught in both years, supports the idea that the steep increase in the number of frogs estimated is due to recently produced tadpoles metamorphosing into frogs and not due to immigration from other water bodies.

4.2. Results of parameter estimation

In this section, we perform two experiments with two different distributions of birth rates. The first assumes that b_t is a uniform distribution representing the mean number of tadpoles produced by a breeding frog during the breeding season and zero otherwise. The second experiment uses a birth distribution based on field calling data.

For the number of data points n we consider two cases. For the first case, we use the full time-series for 2004 and 2005, with $n = 34$. In the second case, we assume that the three data points with the highest population estimates are outliers and do not include them in the estimation procedure, so $n = 31$. An argument suggesting that these values may be outliers has been discussed in detail for the 2004 case in Pham et al. (2007).

In particular, from Fig. 3, it is clear that the 95% confidence intervals for the high population estimates of weeks 18 and 19 in 2005 are considerably larger than the other weekly estimates. The same is true for week 11 in 2004 (Pham et al., 2007). This is due to the fact that during these weeks the recapture rates were very low in comparison with other weeks. Thus, explaining our reasoning for treating these three points as “outliers” in some of the fitting experiments.

4.2.1. Uniform distribution for birth

Here we assume that the birth is uniform across the breeding season and we set $b_t = 11.538$ tadpoles per week per breeding frog (300 per season) (see Fig. 4). In Table 2, we present the parameter estimates obtained from the least-squares method for the first case where all the data points are used (i.e., $n = 34$) together with standard errors. Using these estimates, in Fig. 5(a), we present the total number of frogs F_t obtained from the numerical solution of model (1) superimposed on the frog (breeders and non-breeders) population estimates obtained from 2004 to 2005 field datasets. It can be seen from this figure that the model fits the dataset well. We then ran the model for a longer period of time (500 weeks) using the parameter values for the full dataset given in Table 2 and pre-

Table 2
Weekly least-squares parameter estimation results (with and without outliers) for the two distributions of birth rate.

Parameter	Outliers included	Uniform birth distribution		Birth distribution according to calling data	
		Estimate	S.E.	Estimate	S.E.
a_1	Yes	0.5558	0.1307	0.5793	0.1888
k_1	Yes	0.0000	0.0001	0.0000	0.0001
a_2	Yes	0.9827	0.2096	0.9999	0.0976
k_2	Yes	0.0003	0.0009	0.0002	0.0004
a_3	Yes	0.8806	0.3167	0.8943	0.4040
k_3	Yes	0.0000	0.0009	0.0000	0.0009
a_1	No	0.5422	0.1540	0.6111	0.2167
k_1	No	0.0000	0.0002	0.0001	0.0003
a_2	No	0.9999	0.2295	0.9999	0.1491
k_2	No	0.0003	0.0012	0.0002	0.0006
a_3	No	0.9002	0.3362	0.9203	0.4280
k_3	No	0.0000	0.0012	0.0000	0.0014

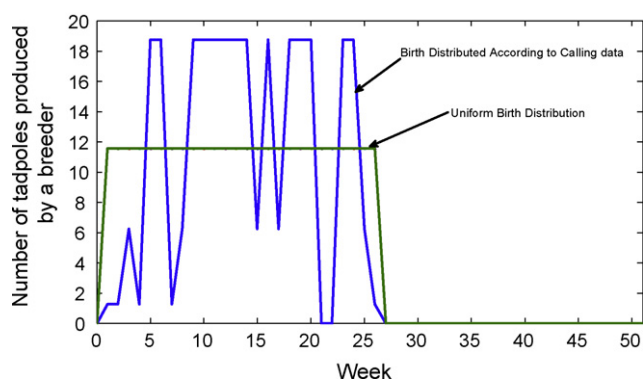


Fig. 4. Birth rate distributed according to calling data superimposed on uniform birth distribution.

sented the results for the breeders and non-breeders in Fig. 5(b) and for tadpoles in Fig. 5(c). It is clear that in this case the population converges to a periodic solution. In fact, the period is 1 year long.

For the second case, we remove the outliers from the estimation process (i.e., $n = 31$), we provide the parameter estimates in Table 2 (bottom part) with the corresponding standard errors. In Fig. 5(d), we present the total number of frogs F_t obtained from the numerical solution of the model (1) superimposed on top of the frog population estimates obtained from 2004 to 2005 data. We then present the long-term behavior for breeders and non-breeders in Fig. 5(e) and for tadpoles in Fig. 5(f), using the same parameter estimates used in Fig. 5(d). Once again, the population converges to a periodic solution. The comparison of the least-squares value L for the full dataset and the outlier omitted dataset is in Table 3.

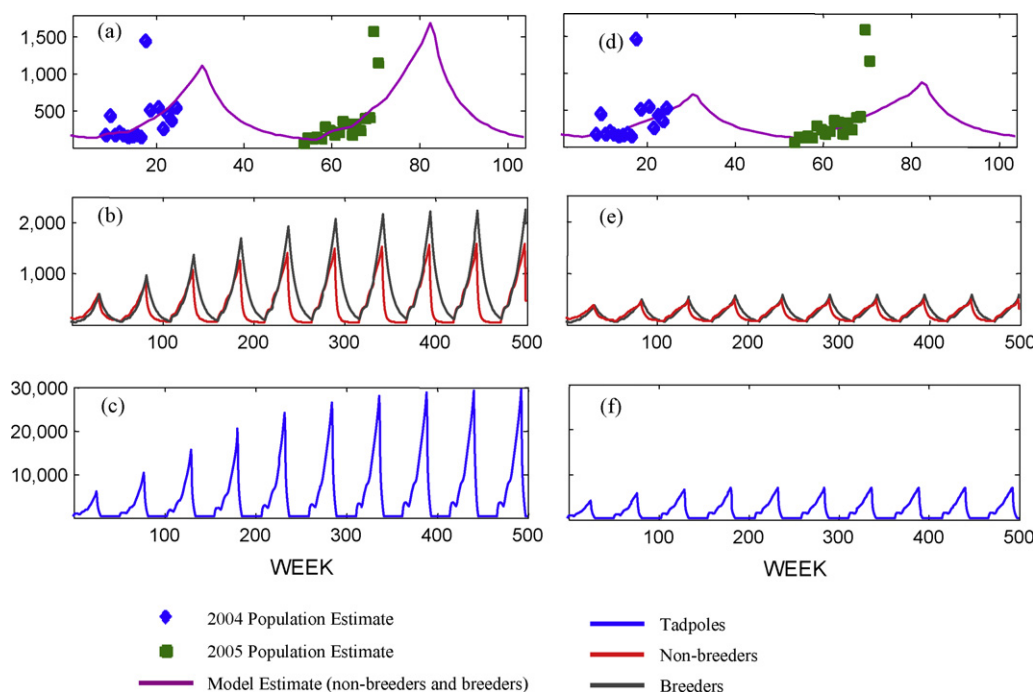


Fig. 5. (a) Total frog numbers (breeder and non-breeders) predicted by the model (1) (using the parameters estimates resulting from the least-squares approach with outliers) with uniform birth distribution (purple line) superimposed on estimated total frog number resulting from the data collected in 2004 (blue diamonds) and 2005 (green squares). (b) The model predicted long-time behavior of breeders (grey line) and non-breeders (red line) with parameter estimates resulting from the least-squares method with outliers. (c) The model predicted long-time behavior of tadpoles with parameter estimates resulting from the least-squares method with outliers. (d) Total frog numbers predicted by the model (1) (using the parameters estimates resulting from the least-squares approach without outliers) with uniform birth distribution (purple line) superimposed on estimated total frog number resulting from the data collected in 2004 (blue diamonds) and 2005 (green squares). (e) The model predicted long-time behavior of breeders (grey line) and non-breeders (red line) with parameter estimates resulting from the least-squares method without outliers. (f) The model predicted long-time behavior of tadpoles with parameter estimates resulting from the least-squares method without outliers. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of the article.)

Table 3
Comparison of the of least-squares function, L , for each dataset type with the two birth distributions.

Dataset type	Uniform birth distribution		Birth distribution according to calling data	
	Calculated value for L	L divided by number of data points	Calculated value for L	L divided by number of data points
Full dataset	9.5292	0.2803	10.8059	0.3178
Data omitting outliers	4.7381	0.1528	6.3955	0.2063

4.2.2. Birth distributed according to male frog calling data

Using the calling data of 2005 and 2006 we derived a birth distribution as follows: for intensity level 0 we assumed no frogs were reproducing; for intensity level 1 we assumed one frog was reproducing; for intensity level 2 we assumed that five frogs were reproducing and for intensity level 3 we assume that 15 frogs were reproducing. In this case we still maintained an average of 300 tadpoles per breeding adult for the entire breeding season. However, in this case the 300 tadpoles are not uniformly distributed across the 26-week breeding season, but rather distributed according to the calling data (see Fig. 4).

With this birth rate we repeated the parameter estimation experiments with outliers ($n = 34$) and without outliers ($n = 31$) and presented the parameter estimates in Table 2. In Fig. 6 we show the model-to-data fits and present the long-term behavior of the model for resulting parameter values. The comparison of the least-squares value L for the full dataset and the outlier omitted dataset is in Table 3.

4.3. Model sensitivity analysis

In this section we present results for the sensitivity of the model output to the survivorship of eggs, tadpoles, non-breeders and breeders. Recall that in deriving the standard errors for the param-

eter vector q we had to compute the sensitivity of the quantity F_t (total number of breeders and non-breeders at time t) with respect to the parameter q which includes the survivorship of tadpoles, non-breeders and breeders (see the matrix $X(q)$ given in Eq. (8)). Here, for convenience of the reader, we provide the graphs of the sensitivities of this quantity F_t to these inherent survivorships denoted by a_1, a_2 and a_3 . Furthermore, we will present the sensitivity of F_t to the eggs survivorship denoted by a_0 . In particular, we consider the case where the birth is distributed according to calling data and in Fig. 7 we plot the derivative of the function F_t with respect to each of these survivorships as a function of time over approximately 10 years, i.e., we plot the quantities $|\partial F_t / \partial a_1|, |\partial F_t / \partial a_2|$ and $|\partial F_t / \partial a_3|$ for $t = 1, 2, \dots, 520$ evaluated at the estimated parameters obtained for the full dataset and for the dataset omitting outliers (see Table 2) and the quantity $|\partial F_t / \partial a_0|$ for $t = 1, 2, \dots, 520$ evaluated at the $a_0 = 0.5$ used in our simulations. To compute these derivatives we apply a forward difference approximation as that presented in Eq. (6). The results show that for the parameter estimates resulting from the full dataset, the quantity F_t which is obtained from solving the model (1) is most sensitive to the inherent survivorship of breeders then to the inherent survivorship of tadpoles. However, it is much less sensitive to inherent survivorship of non-breeders and survivorship of eggs. For the parameter estimates resulting from the outlier

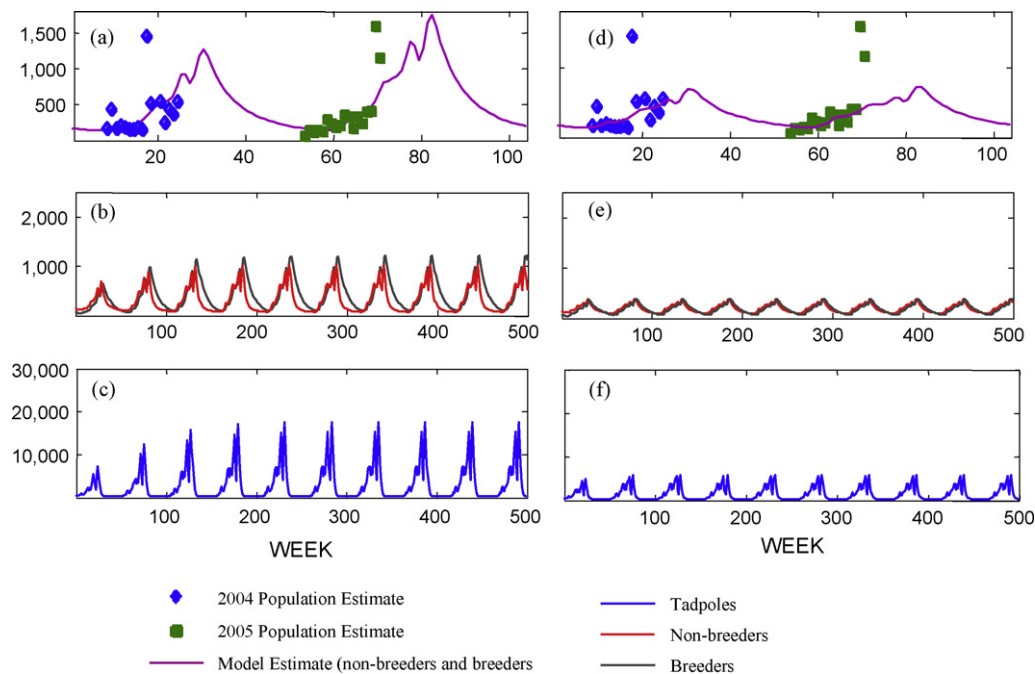


Fig. 6. (a) Total frog numbers predicted by the model (1) (using the parameters estimates resulting from the least-squares approach with outliers) with birth rate distributed according to calling data (purple line) superimposed on estimated total frog numbers resulting from mark-recapture data collected during 2004 (blue diamonds) and 2005 (green squares). (b) The model predicted long-time behavior of breeders (grey line) and non-breeders (red line) with birth distributed according to calling data and parameters estimates resulting from least-squares approach with outliers. (c) The model predicted long-time behavior of tadpoles with birth distributed according to calling data and parameters estimates resulting from least-squares approach with outliers. (d) Total frog numbers (using the parameters estimates resulting from the least-squares approach without outliers) with birth rate distributed according to calling data (purple line) superimposed on estimated total frog numbers resulting from mark-recapture data collected during 2004 (blue diamonds) and 2005 (green squares). (e) The model predicted long-time behavior of breeders (grey line) and non-breeders (red line) with birth distributed according to calling data and parameters estimates resulting from least-squares approach without outliers. (f) The model predicted long-time behavior of tadpoles with birth distributed according to calling data and parameters estimates resulting from least-squares approach without outliers. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of the article.)

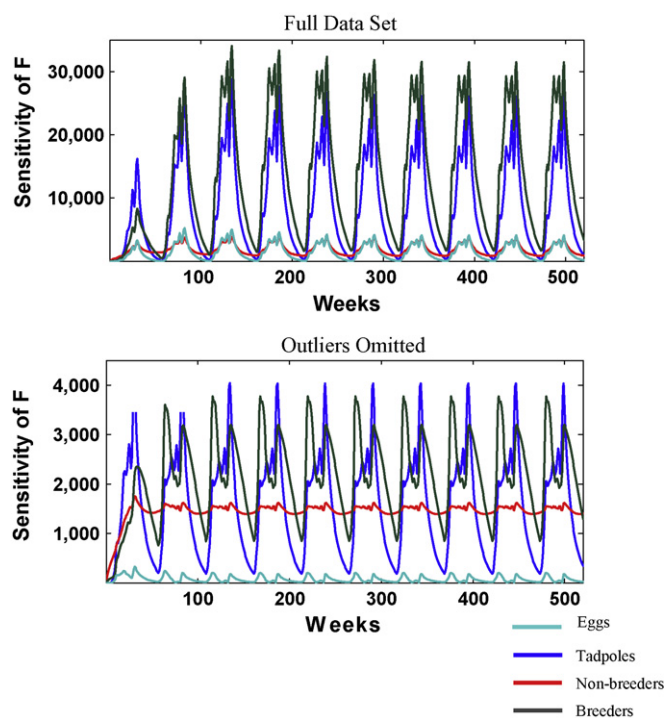


Fig. 7. The sensitivity of the frog population F_t to survivorship values of eggs (cyan line), tadpoles (blue line), breeders (grey line) and non-breeders (red line) for the following two cases: (a) full dataset and (b) dataset with outliers omitted. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of the article.)

omitted dataset, the quantity F_t is most sensitive to the inherent survivorship of breeders then to the inherent survivorship of tadpoles. It is a little less sensitive to the inherent survivorship of non-breeders and much less sensitive to survivorship of eggs. Similar results hold for the case of uniform birth distribution. These conclusions will be more evident in the next subsection which focuses on the development of a stochastic version of the model (1) which accounts for stochastic annual variation in the parameters.

4.4. Stochasticity and extinction

We are interested in understanding how sensitive the model output, which predicts persistence of the population in the long term when using the estimated inherent survivorship values, to annual stochastic variation in these inherent survivorship estimates. Here, we consider the following stochastic version of the model (1): For each simulation we vary one parameter and fix the remaining parameters. At the beginning of each year we randomly choose a value for the varying parameter from the interval $[q^* - fq^*, q^* + fq^*]$ where q^* is the parameter estimate obtained in the fitting experiments above (see Table 2) and $0 < f < 1$ represents maximum percentage change in that parameter (for example $f=0.2$ implies the parameter is allowed to vary up to 20% of its estimated value). If the right hand side of the interval exceeds the biologically relevant survivorship value of 1 then this interval is truncated at that value. In our experiments we choose $f=0.1, 0.15, 0.2, 0.25, 0.3$ to represent a maximum change of 10%, 15%, 20%, 25% and 30% in the parameter value estimated. We perform several sets of 500 sample paths where each sample path is run for 10 years. For each set of 500 sample paths, we vary one parameter and fix the remaining ones. During each path simulation, if at any time the total number of frogs (breeders and non-breeders) falls below 2 then we consider the population extinct. At the end we divide the number of

Table 4
Probability of extinction over 10 years.

Parameter	Dataset type	$f=0.1$	$f=0.15$	$f=0.20$	$f=0.25$	$f=0.30$
a_3	Full dataset	0.000	0.130	0.552	0.824	0.930
	Data omitting outliers	0.000	0.004	0.228	0.618	0.850
a_1	Full dataset	0.000	0.000	0.000	0.004	0.040
	Data omitting outliers	0.000	0.000	0.000	0.000	0.000

extinct sample paths by the total number of paths (500) to obtain an extinction probability. Subtracting the extinction probability from 1 provides us with a persistence probability for this population. The results of these simulations for the birth distributed according to calling data are presented in Table 4 for the survivorship of breeders and for the survivorship of tadpoles. Similar results hold for the case where birth is distributed according to calling data. We point out that up to 30% stochastic variation in eggs and non-breeder survivorships leads to all sample paths being persistent, i.e., zero probability of extinction; thus we do not present these results in Table 4. Furthermore, up to 10% variation in breeder survivorship and up to 20% variation in tadpole survivorship also lead to all sample paths being persistent (i.e. zero extinction probability). From the results in Table 4 it can be concluded that the model is most sensitive to stochasticity in the inherent survivorship of breeders leading to 55% of the sample paths going extinct for the full dataset (and 22% of the sample paths going extinct for the dataset omitting the outliers) when this parameter is allowed to change 20%.

5. Discussion

The intra-annual patterns observed in 2005 were the same as those observed in 2004. While the marking techniques were different in 2004 and 2005, because both used subcutaneous fluorescent plastic tags we feel they are comparable when the data are analyzed using the hypergeometric statistical method to derive population estimates. The frog population size (breeders and non-breeders) and average body length of *H. cinerea* varied during 2005. In April and May of 2005, the frog population was smaller in number and larger in average size than the frog population in late August. A significant increase in frog population occurred in August and was associated with the influx of recently metamorphosed frogs into the population. The observed intra-annual pattern was corroborated by a three-stage life history model with seasonal breeding. Though the population fluctuates significantly over the course of a growing season, the model predicts that the population is stable over the long-term provided that the actual adult survivorship is within 10% from the estimated value. If it is within 15% then the model predicts a 13% probability of extinction within 10 years period. The model output which predicts persistence for the estimated parameter values is far less sensitive to the inherent survivorship of tadpoles and minimally sensitive to the inherent survivorship of non-breeders. In the fact, the model predicts a probability of extinction of 4% if the tadpoles survivorship is within 30% of the estimated value and no extinction is possible if the survivorship of non-breeders is within 30% of the estimated value. Furthermore, our stochastic simulations show that if the 50% eggs survivorship that we assumed in our simulation increases or decreases by up to 30% then the stochastic model predicts zero probability of extinction, i.e., the model output is pretty robust to such changes in egg survivorship.

Population parameters estimated using the least-squares approach were survivorships for adults, juvenile frogs and tadpoles as well as density effects. We used parameters from the literature to estimate egg production. Egg production is one of the more reliable parameters from the literature since *H. cinerea* are regularly bred in

captivity. Thus, the parameter estimation was based primarily on our mark-recapture data and the model structure. It worth pointing out that, to the best of our knowledge, this and Pham et al. (2007) are the only studies providing population estimates of *H. cinerea*. Furthermore, this study is the first to use frequent population estimates to parameterize a population dynamics model.

In 2005, we captured and marked *H. cinerea* from 29 April to 16 September. The study from the previous year ran from 17 June to 22 October. Fig. 3 shows a sharp increase in the population estimates of frogs caught on the week of 10 September 2005. In 2004, there was also an increase around the week of 27 August (Pham et al., 2007). In 2004 and 2005, the mean lengths of the frogs caught each week declined coincidentally with a sudden increase in our population estimates (Table 3, Pham et al., 2007). During this increase in population we also began catching froglets (frogs whose tails were not yet fully absorbed). These lines of evidence strongly suggest an influx of recently metamorphosed frogs from the pond into the population. Furthermore, the timing of this increase matches well with noted increases in calling intensity earlier in the year and what is known about egg and tadpole natural history. This hypothesis is also supported by our models.

During the breeding season adult males call, and since we use calls to help locate individuals our method is biased towards males at the height of the breeding season. We do not know how strong the bias is, but assume that if the sex ratio is 1:1 we are underestimating the adult population size. Froglets and juvenile frogs generally do not vocalize and are less likely to have a sex ratio bias. However, we were unable to develop a satisfactory method for consistently determining the sex of frogs in the field.

The model-to-data fitting experiments provide us with estimates on inherent survivorship rates and density-dependence effects on such survivorships (the estimate of the parameter q). The estimates in Table 2 suggest a weekly survivorship rate of 54–61% for tadpoles, 98–99% for non-breeders, and 88–92% for breeders. Furthermore, they suggest that the survivorship of breeders show minimal density dependence, while that of juveniles and tadpoles are influenced by density slightly.

Comparing the parameter estimates resulting from using the full dataset (Table 2, top part) with the estimates resulting from using the dataset omitting the outliers (Table 2, bottom part), one observes that the density effect on tadpoles is slightly higher for the dataset omitting the outliers. Also the L value divided by the total number of points is lower for the set of parameter estimates without outliers (Table 3), suggesting a better least-squares fit. Furthermore, the long-time behavior of the model when omitting the outliers results in lower population numbers than the ones with the full dataset. These numbers are, although still a little higher, closer to the current population estimates. Also the long-time behavior of the population using estimates resulting from the birth distribution based on calling data (Table 2) results in lower population numbers when compared with the uniform birth distribution case (Table 2) which are closer to the population estimates we obtained during 2004–2005.

There were several important parameters we were unable to measure in the field. First, we were unable to estimate tadpole population size. This necessitated that we use values from the literature on tadpole production (tadpoles produced per female frog) and then use the model to back estimate tadpole survivorship. Second, we do not have information on life stage based carrying capacity or predation rate for any of the individual ponds in the system, but this may be important. For example, differences in the numbers of frogs captured in the different ponds may be a function of available high quality habitat or differences in their predator communities. Third, we treated the ponds in the complex as one large population. In 2005 we recorded 10 out of 76 recapture events where indi-

viduals switched ponds (J. Carter, unpublished data). This nominal 13% exchange rate may indicate that the entire complex may more accurately be described as a meta-population, with different survivorship and fecundity rates in the different ponds. Unfortunately, the numbers captured were insufficient to allow parameter estimation on a per-pond basis. However, the above limitations have been present in many previous studies estimating the size and survival rates of amphibian populations (Bradford et al., 2004; Grafe et al., 2004; Anholt et al., 2003; Bailey et al., 2004; Govindarajulu et al., 2005).

This study is unique for two reasons. First this study, together with Pham et al. (2007), is the first to make weekly estimates throughout the breeding season for *H. cinerea* and the first to do so for an urban area. Second, this is the first study to explicitly tie population estimates for *H. cinerea* to a population dynamics model. This modeling allowed us to estimate parameters such as tadpole and frog survivorship rates that currently we are unable to directly measure. The graphical results of the model suggest that these stage/age structured models describe the dynamics reasonably well and thus may be used as tools for understanding the long-time behavior of this population.

Our models predict that if the estimated parameters vary up to 10%, the population of *H. cinerea* at the Federal Complex should exhibit long-term persistence barring a major disruption of the habitat. This conclusion is in accord with the observation that *H. cinerea* have been observed at the Federal Complex since 1997. While these populations may persist long-term, the estimated number may vary by an order of magnitude during the active season and may experience significant changes over short periods of time.

6. Concluding remarks

H. cinerea population dynamics have high amplitude oscillations but appear to be persistent over several years. This was evidenced by the capture–recapture data and corroborated by the site history and our model prediction using up to 10% variation in the estimated parameters. Monitoring is a critical part of population management, especially for endangered and threatened species. It is suggested that anuran monitoring efforts should take into account these natural intra-annual variation in population size.

This will allow us to determine if the population of interest is increasing, decreasing or stable. Many anuran populations like the *H. cinerea* in this study, experience large seasonal changes in population size. Therefore the timing of when to make the population estimate is critical for species with similar life history patterns. A mismatch in timing from year-to-year could lead to mistakes in assessing the status of the population of interest.

Because of logistical constraints, monitoring programs are often time limited and cannot be conducted through out the entire breeding season. Using a population dynamics model we can estimate the health and stability of a population by sampling two times during the year. First, early in the season after all the individuals have reached the breeding pools but well before the first tadpoles have metamorphosed to froglets. The second sampling period should be shortly after the peak of when the tadpoles have metamorphosed to froglets. These two time frames can give an estimation of the breeding population size and breeding success. Data on frog call monitoring, which is easier to collect than mark-recapture data, can be used to estimate when the second sampling session should begin because the length of time from eggs being laid to metamorphosis from tadpoles to juveniles is generally known and species specific. If conducting a mark-recapture study is only possible once a year, then the first time frame should be used. That mark-recapture

should be timed to the peak of breeding activity in order to get an estimation of the breeding pool population size for that year and to make projections for the next. This sampling principle can be applied generally to all species with a similar life-history pattern, where large seasonal swings in population sizes are due to seasonal breeding patterns.

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